INTRASPECIFIC VARIATION IN PASSERINE BIRD SONGS

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The vocalizations of birds are of interest to ornithologists because of the role they play in behavior, and because of their value in species recognition. These vocalizations are subject to intraspecific variation, but the accurate study of this variation involves somewhat different techniques than are involved in the study of morphological variation. Developments in recording and sound-analyzing equipment in the last fifteen years or so have made it possible to study variation in bird vocalizations with a degree of accuracy comparable to that of morphological studies.

My colleagues and I at Ohio State University have been making tape recordings of bird songs since 1948, and we now have over 4,400 recordings, representing nearly 250 species. A great many of these have been analyzed by means of a sound spectrograph, and while we may not have as many recordings as we would like, to make a thorough study of variation in any species, perhaps enough recordings have been obtained and analyzed to present some general points regarding the intraspecific variation in the songs of birds in the order Passeriformes.

An individual bird may produce a variety of sounds; we are concerned here with the particular vocalizations of passerine birds that are called *songs*. Song may be defined as the vocalizations, usually given only by the male and usually more complex in character than the bird's various call notes, which appear to have one or more of three principal functions: (1) to advertise the presence of the male, (2) to attract a female, and (3) to repel other males of the same species. The distinction between song and other vocalizations is not always sharp, partly because the songs of some birds may be of a relatively simple character and not very different from the bird's other vocalizations, and partly because the exact function of many vocalizations is not clearly understood. Most of the songs discussed in this paper are termed advertising or territorial songs by many ornithologists.

Theoretically, many sorts of variation might occur in passerine song. Song might vary in an individual bird, in different individuals of a local population, and/or in the birds of different (geographically separated) populations. The songs of an individual might vary with age, time of day, season of the year, the presence of other birds, or other factors. Different individuals, either in a local population or in geographically separated populations, might sing songs of different patterns, or show different preferences for a limited number of song patterns.

SONG DEVELOPMENT IN THE INDIVIDUAL

A male passerine bird usually begins to sing when it is several months old, and thereafter sings principally (or solely) during the breeding season. In species where different individuals sing essentially the same song it is probable that the song patterns are largely hereditary, but in species where different individuals sing somewhat different songs (the situation in the majority of passerine birds), it is probable that at least some features of the songs are learned by listening to other birds. The role of learning in song acquisition has been pointed out by a number of investigators, including Thorpe (1951, 1954, 1956, 1958*a*, 1958*b*), Koehler (1951), Poulsen (1951, 1958), and Lanyon (1957, 1960).

The early season singing of birds whose song patterns are at least in part learned is somewhat atypical; the patterns are erratic and somewhat abortive, and the birds sound as though they were trying to decide just what patterns to sing, and to perfect their singing technique. Later in the season, as the bird perfects its song patterns, little of this type of singing is heard. Many passerine birds that sing during their migration sing songs that are a little different (e.g., more variable, with the patterns less well defined) from the songs sung by these birds on their nesting grounds; such birds are probably in the "perfecting" stage of their song development. Once the bird's song patterns are perfected they appear to be largely fixed for the rest of the bird's life; there appears, based on my study of the songs of a number of individual birds over periods of two to four years, to be relatively little variation from year to year in the song patterns of a given individual.

Our collection of bird recordings contains a number in which the songs are very atypical for the species, and closely resemble the songs of another species. Some birds rather regularly mimic the songs and calls of other species (the Mockingbird and Starling are well known examples), but occasionally other birds—species not generally considered mimics—will do this. Tasker (1955), for example, reports a Chipping Sparrow with the song of a Clay-colored Sparrow, and Hulme (1950) reports a Chaffinch mimicking the song of a Hedge Sparrow. Among our recordings of such atypical mimicry are recordings of a Rufous-sided Towhee and a Bachman's Sparrow singing Field Sparrow songs, a Field Sparrow singing a song similar to that of a Prairie Warbler, and a Red-eyed Vireo singing towhee-like songs. I have seen a Blue Jay that was exposed since it left the nest only to Robin song, and which sang a robin-like song. It seems likely that these cases of mimicry are the result of the bird learning its song from another species.

LOCAL VARIATION

Different species of passerine birds differ in the amount of variation in the songs of a given individual and in the songs of different individuals. The

TABLE 1

AN OUTLINE OF THE INTRASPECIFIC VARIATION IN THE ADVERTISING SONGS OF PASSERINE BIRDS

Songs of a Given Individual	Songs of Different Individuals			
	Of the Same Pattern	Of a Few Different Patterns	Of Many Different Patterns	Of Many Different Patterns
		Much Overlapping	Some Overlapping	Little or No Overlapping
Of One Pattern	Least Flycatcher Traill's Flycatcher*	Savannah Sparrow Grasshopper Sparrow	Yellowthroat Chipping Sparrow Slate-colored Junco	
	White-breasted Nuthatch	Ovenbird Kentucky Warbler White-throated Sparrow		
Of a Few Patterns	Wood Pewee Phoebe Traill's Flycatcher*	Black-throated Green Warbler Parula Warbler	White-eyed Vireo	Indigo Bunting Field Sparrow Vesper Sparrow
	Blue-winged Warbler		Tufted Titmouse Cerulean Warbler American Redstart	
Of Many Patterns			Rufous-sided Towhee Carolina Wren Cardinal Bachman's Sparrow	Wood Thrush Hermit Thrush Song Sparrow Lark Sparrow

* The reason for Traill's Flycatcher appearing in two places in this table is discussed on p. 74.

types of intraspecific variation found in the advertising songs of a number of passerine birds are outlined in Table 1. This table does not include species that sing more or less continuous songs, such as the Catbird, Brown Thrasher, and Red-eyed Vireo, because the songs of these species have not yet been studied in sufficient detail; such species would probably fit somewhere in the lower right-hand part of the table. Most passerine birds that sing short isolated songs (in contrast with more or less continuous songs) would probably fit into one of the four top center squares. Most nonpasserine birds probably fit in the left-hand square in the top row.

The songs of some species consist of a definite sequence of notes and phrases, and the different songs of a particular pattern sung by a given individual are practically identical; in other species, where all or part of the song consists of a series of similar notes or phrases, different songs of a particular

pattern sung by a given individual may differ in the number of such notes and phrases. In the squares of Table 1 containing a broken line, the different songs of a particular pattern sung by a given individual of the species above the broken line are practically identical, but in the species below the broken line the number of notes or phrases in different parts of the song may vary. In squares with no broken line, the different songs of a particular pattern sung by a given individual of all the species listed are subject to variation in the number of notes or phrases they contain.

In some species of passerine birds (for example, the species listed in the top row of the table) the songs of a given individual are all of the same pattern; in others (the species listed in the middle row of the table) each individual may sing songs of two to five different patterns; in still other species (those listed in the bottom row of the table) each individual may sing songs of six or more different patterns.

The greatest amount of variation in the songs of a given individual was found in the species listed in the bottom row of Table 1. The maximum number of song patterns in our recordings of a single individual is 8 for a Rufous-sided Towhee (Borror, 1959*a*), 11 for a Cardinal, 13 for a Song Sparrow, 13 for a Hermit Thrush (Borror, 1960), 18 for a Wood Thrush (Borror and Reese, 1956), 22 for a Carolina Wren (Borror, 1956), 37 for a Bachman's Sparrow, and 58 for a Lark Sparrow. Variation within patterns occurred in all these species. The songs of a given pattern in the Song Sparrow, for example, may vary in the number of phrases of a given type in different parts of the song, in the presence or absence of certain notes or phrases, in where (along a certain sequence of notes and phrases) the song ends, and/or in the particular types of phrases with which the song begins or ends; the variation in Song Sparrow songs is such that the delimitation of patterns is occasionally somewhat arbitrary. In the 462 songs we have recorded from one Maine Song Sparrow, which had 13 distinct song patterns, there were 187 different songs.

In some species (those listed in the left-hand column of Table 1) the songs of different individuals are of the same pattern, with only slight individual differences (see Figs. 1, 4, and 5). In other species (those listed in the second column of the table) the songs of different individuals are occasionally of different patterns, but our recordings do not contain more than 12 different song patterns for any of these species; it is quite common ("much overlapping" is the way this is described in the table) to hear different individuals singing songs of the same pattern. In still other species (those listed in the third column of the table) the songs of different individuals are usually different, and our recordings contain more than 12 patterns for each of these species; it is only occasionally that one hears different individuals singing songs of the same pattern. In still other species (those listed in the right-hand

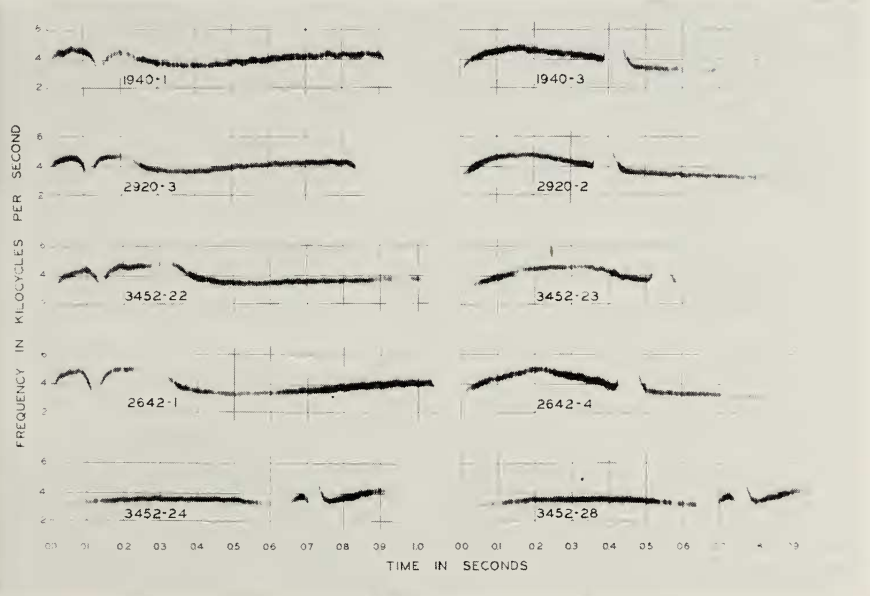

FIG. 1. Audiospectrographs* of Wood Pewee songs. The four upper graphs on the left are of *pee-ah-wee* songs, the four upper graphs on the right are of *peee-ah* songs, and the two graphs at the bottom are of *aaah-didi* songs; 3452 is a recording of the daybreak song, and the other recordings are of daytime songs. 1940, New Albany, Ohio, 26 May 1956; 2920, Lincoln Co., Maine, 30 June 1957; 3452, Bloomington, Indiana, 1 June 1958; 2642, Franklin Co., Ohio, 15 May 1957.

column of the table), our recordings of which contain many different patterns, one rarely if ever hears different individuals singing songs of the same pattern.

The greatest amount of variation in the songs of a given species was found in the birds listed in the right-hand column of Table 1. Our recordings do not contain any instance of two different birds singing songs of the same pattern in the cases of the Indigo Bunting, Vesper Sparrow, Wood Thrush, Hermit Thrush, or Lark Sparrow, and only a few such instances in the cases of the Field Sparrow and Song Sparrow. The different patterns of Field Sparrow songs are fairly similar, and the delimitation of these patterns is somewhat subjective; with a fairly strict delimitation of patterns, only about 2 per cent of our Field Sparrow recordings represent cases of a given pattern being sung by different individuals. The song patterns of the other

* The recordings from which the song graphs in this paper were made are in the collection of recorded animal sounds of the Department of Zoology and Entomology, Ohio State University. I made them all with a Magnemite recorder, Model 610-E, using a tape speed of 15 inches per second; the graphs were made with a Vibralyzer. The first of the two numbers on each graph is the number of the recording, and the second (unless otherwise indicated) is the song in the recording, from which the graph was made.

species in this column differ more than those of the Field Sparrow, and can generally be more objectively delimited, but except for the Song Sparrow we do not have a large number of recordings of any of these species.

Of the 501 recordings we have of Song Sparrows, 356 are from 46 birds in an area of about 40 acres in Maine, and were obtained over a period of several seasons. These 356 recordings contain 2,868 songs, of about 200 patterns (the exact number depends somewhat on how strictly the patterns are delimited). We have over a hundred songs from each of eight different birds from this area, and in these eight birds the number of song patterns per bird varied from 6 to 13 (average, 8.25). Taking into account the variations within patterns, there were 1,494 different songs in the 2,868 recorded from these 46 birds; only 6 of the 1,494 variations, and about a dozen of the two hundred patterns, were sung by different birds.

It is probably very unusual, except possibly in the cases of the Field Sparrow and Song Sparrow, to find two individuals of the species listed in the right-hand column of the table singing songs of the same pattern. Cases of two or more individual Song Sparrows singing songs of the same pattern probably occur only within a local population. It may be that in some of these species no two birds ever sing songs of the same pattern.

There is a great deal of variation in song pattern in the species listed in the third column of the table, even though our recordings contain a number of instances of a given pattern being sung by different individuals. For example, we have 138 different song patterns in 113 Cardinal recordings, 127 patterns in 12 Bachman's Sparrow recordings (seven birds), 93 patterns in 71 Rufous-sided Towhee recordings (Borror, 1959*a*), 45 patterns in 84 Yellowthroat recordings, and 36 patterns in 86 Chipping Sparrow recordings.

GEOGRAPHIC VARIATION

Any bird observer with a critical ear for patterns in bird songs will note that the song patterns of many passerine birds differ somewhat in different areas, but these differences have been critically studied in only a few species. "Local dialects" have been described for the Chaffinch by Marler (1952), Poulsen (1958), and Thorpe (1954). Lanyon and Fish (1958) have discussed the geographic variation in the songs of the Western Meadowlark, and I have published some data on the geographic variation in the songs of the Carolina Wren (Borror, 1956), the Rufous-sided Towhee (Borror, 1959*a*), and the Chipping Sparrow (Borror, 1959*b*). It may be of interest to mention here a few additional examples, based on my studies.

Bachman's Sparrow (*Aimophila aestivalis*).—The songs of this species typically consist of one or two introductory notes followed by a trill; the introductory notes are relatively long and usually steady in pitch, and the

TABLE 2

CHARACTERISTICS OF THE TRILL IN THE SONGS OF SEVEN BACHMAN'S SPARROWS

Character		3 birds in Ohio	4 birds in Florida
Phrase Length* (in sec.)	Range	0.032–0.220	0.040–0.230
	Average	0.124	0.166
Number of Phrases	Range	1–20	4–11
	Average	8.94	7.67
Number of Different Phrase Types	1-noted	12	2
	2-noted	34	15
	3-noted	22	23
	4-noted	1	12
	Total	69	52
Average number of notes per phrase		2.17	2.87
Total number of songs recorded		447	81

* Phrase length is the length of time from the beginning of one phrase to the beginning of the next; the reciprocal of this figure is the number of phrases per second.

trill consists of a rapid series of similar phrases. A given bird may sing songs of a number of different patterns, each pattern consisting of a characteristic introduction and type of trill phrase. In recordings of seven individuals of this species I studied, three from Ohio (*A. a. bachmani*) and four from Florida (*A. a. aestivalis*), and containing 528 songs, there were 127 different song patterns (37 in the songs of one Ohio bird). Several song patterns occurred in the songs of two or three birds in the same state; there was no pattern that occurred in the songs of both an Ohio and a Florida bird. Data on certain features of the trill in the Ohio and Florida songs are given in Table 2; these data indicate that (1) the trill phrases are uttered more slowly, on the average, by the Florida birds than by the Ohio birds (about six per second in Florida songs and eight per second in Ohio songs), (2) the trills in the Florida birds contain, on the average, fewer phrases than those of the Ohio birds, and (3) the trill phrases of the Florida birds contain, on the average, more notes than those of the Ohio birds. (It might be said that the Florida birds had a "southern drawl.")

Song Sparrow (*Melospiza melodia*).—The songs of this sparrow consist of a series of different phrases (mostly 1- to 4-noted), and usually a trill; many of the notes are buzzy. The song begins with a series of similar phrases, either two to four (rarely one or five) uttered at a constant rate, or four to 20 that increase in tempo. A given bird has a vocabulary of a large number of notes and phrases, and these are variously combined to produce up to a dozen or more different song patterns; the different patterns of a given bird

are often quite different. The songs of a given pattern may vary, as noted above (p. 60).

Our Song Sparrow recordings include 388, of some 70 birds, from Maine (*M. m. melodia*); 356 of these are of 46 birds in an area of about 40 acres, and the rest are from varying distances up to 160 miles from this 40-acre area. The vast majority of the songs of the birds in the 40-acre area contain notes and phrases that occur also in the songs of other birds in this area; the songs of birds outside this area contain fewer notes and phrases like those of birds in the area, and the farther away from this area the bird is the fewer the similarities in notes and phrases. In the songs of the Ohio Song Sparrows (*M. m. euphonia*) that have been analyzed to date (of 66 birds, and containing 501 songs of 110 different patterns), the phrases are nearly all different from those of the Maine birds.

Song Sparrow songs are of two general types, those beginning with two to four (rarely one or five) similar and equally spaced phrases, and those beginning with four to 20 similar phrases that increase in tempo; most song patterns can be readily classified into one of these two categories. Songs of the first type were much more common, making up 83.8 per cent of the Ohio patterns and 86.7 per cent of the Maine patterns (these differences in percentage are not significant).

A Song Sparrow apparently has an inborn tendency to sing songs of two general types, but it learns its phrases by listening to other, nearby Song Sparrows. As a result, the songs of different birds in a local population contain similar notes and phrases (but usually arranged differently), while the songs of birds in separated populations contain different phrases. The farther away two populations are, the less likely they are to use similar phrases in their songs.

Cardinal (*Richmondena cardinalis*).—To date I have analyzed 113 recordings of Cardinal songs (containing 946 songs from 100 birds in eight states). These songs consist of 1–43 loud, clear, whistled phrases uttered at rates of 0.9 to 9.0 phrases per second. The songs studied contained 82 different types of phrases (plus a buzzy trill), of which 31 were one-noted, 37 were two-noted, 11 were three-noted, 2 were four-noted, and 1 was five-noted. Cardinal songs may be one-parted, that is, all the phrases alike and uttered at a uniform rate (except possibly the first two or three phrases, which are often slower), or they may contain up to five parts (with the phrases of one part different from those of the next part). The songs are occasionally followed by a buzzy trill (a series of abruptly up-slurred notes, 27–31 per second) that may last up to 1.5 seconds. By giving each phrase type a number, any given song pattern could be represented by one to five numbers (one number for one-parted songs, two for two-parted songs, and so on). The songs of a given bird

may vary in pattern (up to 11 in one Florida bird), and the songs of a given pattern may vary in the number of phrases they contain. There were 138 different patterns in the songs studied, of which 47 were one-parted, 64 were two-parted, 21 were three-parted, 4 were four-parted, and 2 were five-parted.

It is fairly common to hear two Cardinals in a given area singing songs of the same pattern, but it is less common for birds in different areas (i.e., different local populations, in areas separated by four miles or more) to sing songs of the same pattern. Of the 138 patterns found, however, 18 (14 one-parted and 4 two-parted) were sung by birds in different areas; 4 of these were sung by birds in two different states, and 1 pattern was sung by birds in four different states.

The songs of the Ohio birds, *R. c. cardinalis* (797 songs, of 85 birds, and containing 114 song patterns), contained 68 different phrase types, of which 27 were one-noted, 27 were two-noted, 11 were three-noted, 2 were four-noted, and 1 was five-noted; these phrase types averaged 1.87 ± 0.11 notes per phrase. The songs of the Florida birds, *R. c. floridana* (73 songs, of 8 birds, and containing 20 song patterns), contained 20 different phrase types, of which 7 were one-noted, 11 were two-noted, and 2 were three-noted; these phrase types averaged 1.75 ± 0.14 notes per phrase. Ten phrase types (6 one-noted, 3 two-noted, and 1 three-noted) occurred in the songs of both the Ohio and Florida birds. The phrases of the Ohio and Florida birds contained about the same number of notes.

There was no tendency in the songs studied for the birds in different states to sing songs containing a different number of parts. The song patterns in both the Ohio and Florida birds contained an average of 1.9 parts.

Data comparable to the above have been published for a few other species of passerine birds. It has been shown (Borror, 1956) that there are significant differences in the songs of Ohio and Florida Carolina Wrens (representing *Thryothorus ludovicianus ludovicianus* and *T. l. miamensis*, respectively), principally in the phrase rate and the number of phrases in the song: the songs of Florida birds contained, on the average, more phrases and the phrases were uttered more rapidly than in the Ohio birds (the reverse of the situation in the trill of Bachman's Sparrow, described above). In the Rufous-sided Towhee (*Pipilo erythrophthalmus*) it has been shown (Borror, 1959*a*) that the songs of the two subspecies *erythrophthalmus* and *alleni* differ slightly, while the songs of different individuals of the subspecies *erythrophthalmus* as far apart as Ohio and Maine are not significantly different. Studies of Chipping Sparrow songs (Borror, 1959*b*) have shown that there is a great deal of variation in the songs of different birds, but that there is no significant geographic variation within the subspecies *Spizella passerina passerina*, comparing the songs of Ohio and Maine Birds.

In the passerine songs I studied (all from the eastern part of the United States and Canada), there is evidence that in at least some species the songs of different subspecies may differ slightly; within a single subspecies the variation is principally of the sort that might be described as "local dialects," that is, with the birds of different local populations differing in song patterns, but with no significant geographic trends evident.

DIURNAL VARIATION

Most passerine birds sing more consistently in the early morning hours than in the middle of the day; song is usually at a minimum early in the afternoon, and in many species increases again in late afternoon or evening. This phenomenon has been studied in many species, and is apparently correlated with light intensity (Wright, 1912, 1913; Allard, 1930).

A number of birds sing a little differently at daybreak than during the day, and a few sing a little differently at dusk. Distinctive daybreak songs (also called morning twilight songs) have been described for the Wood Pewee (Allard, 1934; Craig, 1943) and for the Crested Flycatcher and the Scissor-tailed Flycatcher (Nice, 1931). We have recordings of distinctive daybreak singing of the Wood Pewee, Crested Flycatcher, and Acadian Flycatcher. There are undoubtedly many other species that sing somewhat differently at daybreak than during the rest of the day. The situation in the Wood Pewee may serve to illustrate the peculiarities of daybreak song.

In its normal daytime singing the Wood Pewee sings songs of two different patterns, *pee-ah-wee* and *peee-ah* (Fig. 1). These two patterns are sung more or less alternately, at the rate of about six or eight a minute; most birds sing about three times as many *pee-ah-wee* songs as *peee-ah* songs. The bird sings a little differently at daybreak; in addition to the two song types just mentioned, it sings a third type, *aaah-didi* (Fig. 1). These three songs are often sung in a definite sequence, at the rate of about 20 songs a minute. This daybreak song begins about an hour before sunrise and lasts about half an hour.

The special daybreak songs of these flycatchers are undoubtedly influenced by light intensity, but their significance to the birds is not clearly understood.

SEASONAL VARIATION

Song is an aspect of bird behavior associated with the breeding season. It begins in the spring, with the onset of the breeding season, usually at a date characteristic for the species. Saunders (1947) presents data on the beginning of song in the spring for a number of species; these dates vary in a given year for different species, and to some extent (usually not more than a week or two) from year to year in a given species. Some species stop or reduce their singing

during certain parts of the nesting cycle, for example, after mating or when they are feeding young; the Song Sparrow ceases singing when it acquires a mate, and begins again when nest building starts (Nice, 1943:118–119).

Song declines after the breeding season and this decline is usually rather gradual, although some species may stop singing rather abruptly. A number of investigators have presented data on the cessation of song in late summer (Bicknell, 1884, 1885; Fry, 1916; Saunders, 1926, 1938, 1948a, 1948b; Baerg, 1930; Vaurie, 1946; Mehner, 1952); the time of cessation varies in different species, and from year to year (as much as two to four weeks) in a given species. The cause of cessation of singing is probably hormonal; cessation usually occurs with the approach of the postnuptial molt.

Some species begin singing again after the postnuptial molt. In general, those species that change color at the postnuptial molt sing in the fall, but the reverse is not always true (Bicknell, 1884; Saunders, 1948). A few species (for example, the Carolina Wren) may sing every month of the year. The songs sung by some species in late fall or winter are often of a rather primitive type (Saunders, 1948), and probably represent "learning" or "practicing" by immature birds (see the discussion on the development of song in the individual, p. 58).

OTHER VARIATION

It might be presumed that, in birds having a number of different song patterns, the different patterns had different meanings to the birds, or particular patterns were sung only under specific circumstances. This may be the case in some birds, but is probably not the case in others; a given type of song or song pattern may serve all the functions of song mentioned above (p. 57), or different functions may be served by different types of songs.

The normal singing rate of a Song Sparrow singing its advertising song is about four to six songs a minute, and it may sing for several minutes at this rate—either from a particular perch or while moving about and feeding. It will sing songs of one pattern for a while, then change to another pattern for a while, then to another, and so on through all or a part of its repertoire. If recorded Song Sparrow songs, of either this same individual or another individual, are played to a bird on its territory, the bird reacts in a characteristic fashion: its singing rate increases to eight or ten songs a minute, and it shows signs of agitation and hops around the speaker. The particular song patterns it sings under these circumstances are the same ones it sings when it is undisturbed; what is changed by the playback is not the bird's song patterns, but its singing rate. I have observed this reaction of Song Sparrows to playbacks on numerous occasions.

Some birds occasionally utter a very soft song that may or may not be of the same pattern as its normal song; such songs are often called secondary

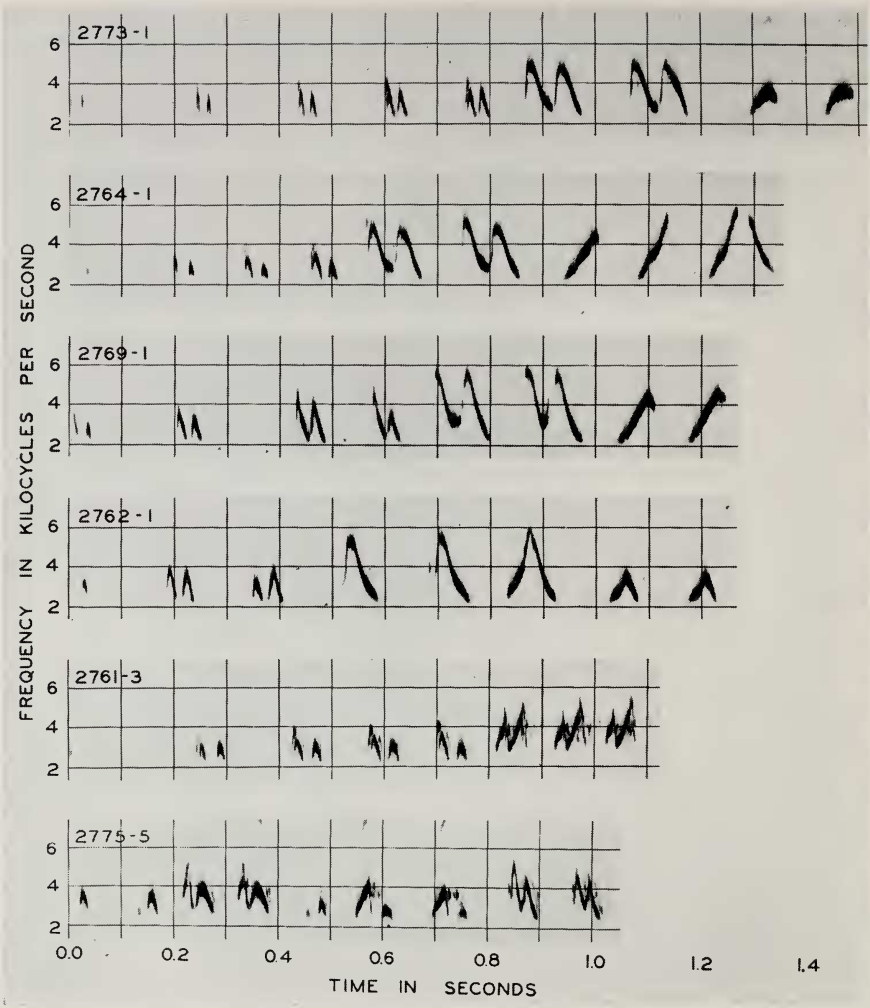

FIG. 2. Audiospectrographs of advertising songs of the Kirtland's Warbler, all from recordings made in Oscoda Co., Michigan, 31 May 1957.

songs, whispering songs, or subsongs (Van Tyne and Berger, 1959:138–139). The significance of such songs is not always clear, but in some species (e.g., the Kirtland's Warbler) these whispering songs appear to function in repelling an intruding male.

A comparison of the advertising and whispering songs of the Kirtland's Warbler is shown in Figs. 2 and 3. The advertising songs of this warbler are of two general types; the songs of one type (the four upper graphs in Fig. 2)

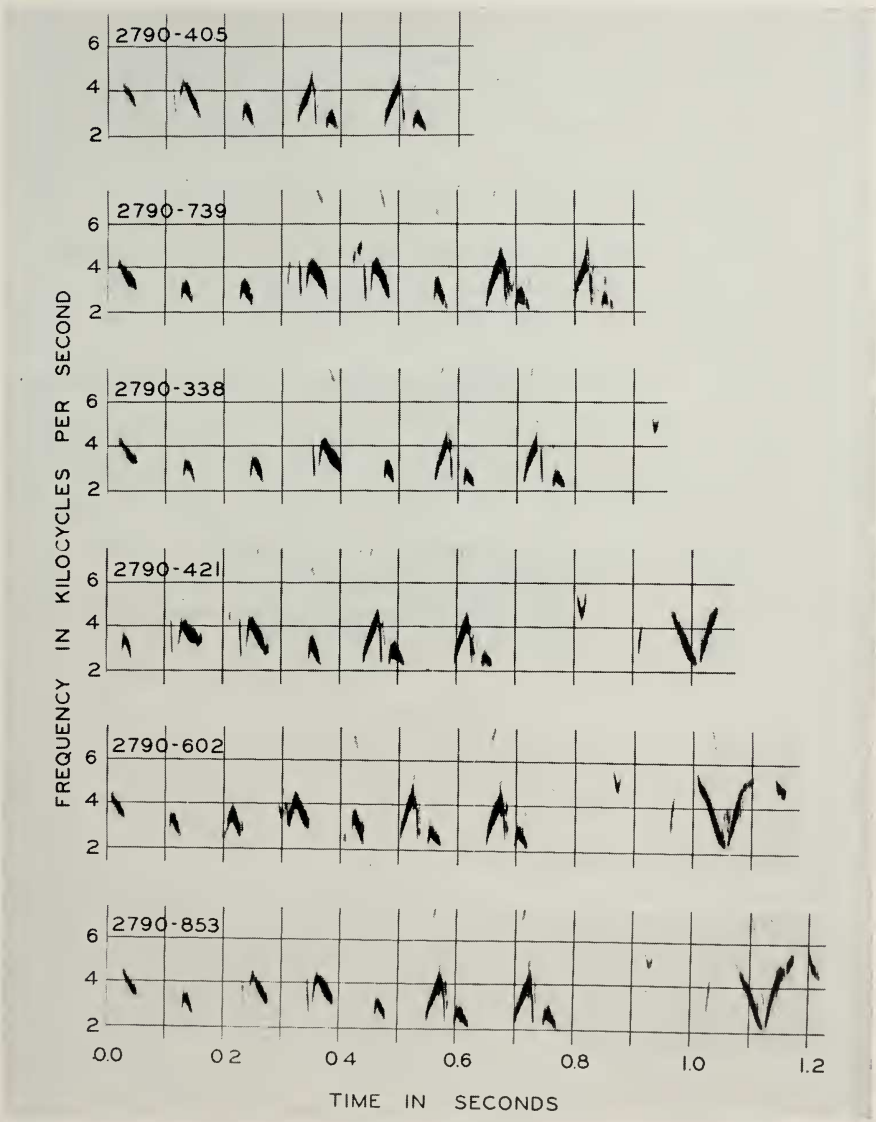

Fig. 3. Audiospectrographs of whispering songs of the Kirtland's Warbler, sung in response to playbacks of the advertising songs on the bird's territory; recorded in Oscoda Co., Michigan, 31 May 1957. The second of the two numbers on each graph is the location of the song in the recording (in minutes and seconds from the beginning).

are somewhat similar in quality and tempo to the songs of the Northern Waterthrush, and the songs of the other type (the two bottom graphs in Fig. 2) are a little like those of a House Wren. Whispering songs (Fig. 3), which

were obtained by playing back a recording of the advertising song on the bird's territory, are much softer than the advertising songs and quite variable in length; they are somewhat similar to the wren-like advertising song.

Many birds have songs which are heard only infrequently, and which are of a somewhat different type than the usual territorial song. The term "flight song" has been used for some such songs (e.g., in the Ovenbird), "twilight song" for others (e.g., in certain flycatchers), and still other terms for others. The biological significance of such songs is known in only a few cases; for example, the "sustained song" of the Grasshopper Sparrow (Smith, 1959), which consists of a typical advertising song followed by a series of buzzes, appears to function in courtship.

Song is primarily a vocalization of the male, but the females of some species may sing occasionally (Nice, 1943:129–132). I have one recording of a female Song Sparrow that was apparently stimulated to sing by playbacks of Song Sparrow songs; its songs were typical for the species, but of a different pattern than any its mate sang. In some species the two sexes sing (the same or different patterns) either simultaneously or alternately. It is not uncommon to hear a pair of Cardinals singing songs of the same pattern (alternately). This type of singing is sometimes called responsive singing, antiphonal singing, or duetting, and occurs in a number of species (Van Tyne and Berger, 1959: 140).

DISCUSSION

Two questions arise with regard to the large amount of intraspecific variation that occurs in the songs of many passerine birds: (1) how the bird student can ever learn to recognize these many song patterns, and (2) the significance of this variation to the birds themselves.

Recognizing Bird Songs.—In most species that sing a number of different song patterns, the patterns are of one or a few general types, and the songs are usually of a characteristic quality. One recognizes the songs of a given species, even patterns he has never heard before, after first becoming familiar with the type(s) of song patterns that species sings and with the quality of the songs. The field identification of bird songs generally involves also some knowledge of what species might be expected to be singing at a given time and place; the importance of this basis of song identification becomes evident when one tries to identify song recordings in the laboratory. If the field observer has an ear for pattern in bird songs, he will eventually be able to recognize individual birds by their songs; this is particularly true for the species listed in the two right-hand columns of Table 1.

Significance of Song Variation to the Birds.—Certain types of songs are known to play a role in courtship or in territorial defense, as we have seen, but the significance to the birds of much of the intraspecific variation in the

advertising songs can for the most part only be guessed. Such data as are available on this point suggest two things, one regarding the ability of the bird to recognize different individuals of its own species, and the other regarding the role played by song in bird speciation.

Individual Recognition.—The advertising songs of an individual Ovenbird are of one pattern (or phrase type), differing only in the number of phrases in the song. One may occasionally find different Ovenbirds with identical phrases, but the songs of different individuals are often different (Table 1). Weeden and Falls (1959) have shown that an individual Ovenbird can distinguish between the songs of different individuals of their species, and can recognize the songs of particular individuals (their neighbors); they react more strongly to songs of nonadjacent birds than to songs of their neighbors. This is apparently a mechanism that reduces strife between birds in adjacent territories once the territorial boundaries are established, and enables the bird to recognize (and possibly cope with) the greater danger of encroachment on its territory by "strangers."

The Role of Song in Speciation.—Song in passerine birds often plays an important role in sexual and species recognition; this has been demonstrated in a number of species (Dilger, 1956; Stein, 1958). Certain vocalizations have been shown to play a similar role in many other animals, including fish (Tavolga, 1956, 1958*a*, 1958*b*; and others), amphibians (Blair, 1955, 1956, 1958; and others), and insects (Alexander, 1957; Alexander and Moore, 1958; Walker, 1957; and others). On the other hand, song in some passerine birds is not the principal means of species recognition; for example in the meadowlarks (*Sturnella magna* and *neglecta*) specific recognition is by call notes rather than song (Lanyon, 1957). Because of the role of song in species recognition, variation in song may lead to speciation; the situation in certain flycatchers may serve to illustrate this point.

An interesting feature of some flycatcher songs is the fact that each individual has two types of songs, or song patterns, which it sings more or less alternately, and different individuals of the species have essentially the same patterns. This is the case, for example, in the Wood Pewee, Phoebe, and Traill's Flycatcher.

The Wood Pewee in most of its singing sings songs of two different patterns, *pee-ah-wee* and *peee-ah* (Fig. 1). These two songs are not sung in any fixed sequence, but a bird generally sings about three times as many songs of the first type as the second.

The Phoebe also sings two types of songs more or less alternately. One type, the "buzz" song (Fig. 4), consists of a slurred note followed by a buzz, and the other, the "sputter" song (Fig. 4) consists of a similar slurred note followed by a sputter. The two types of songs are readily distinguishable by

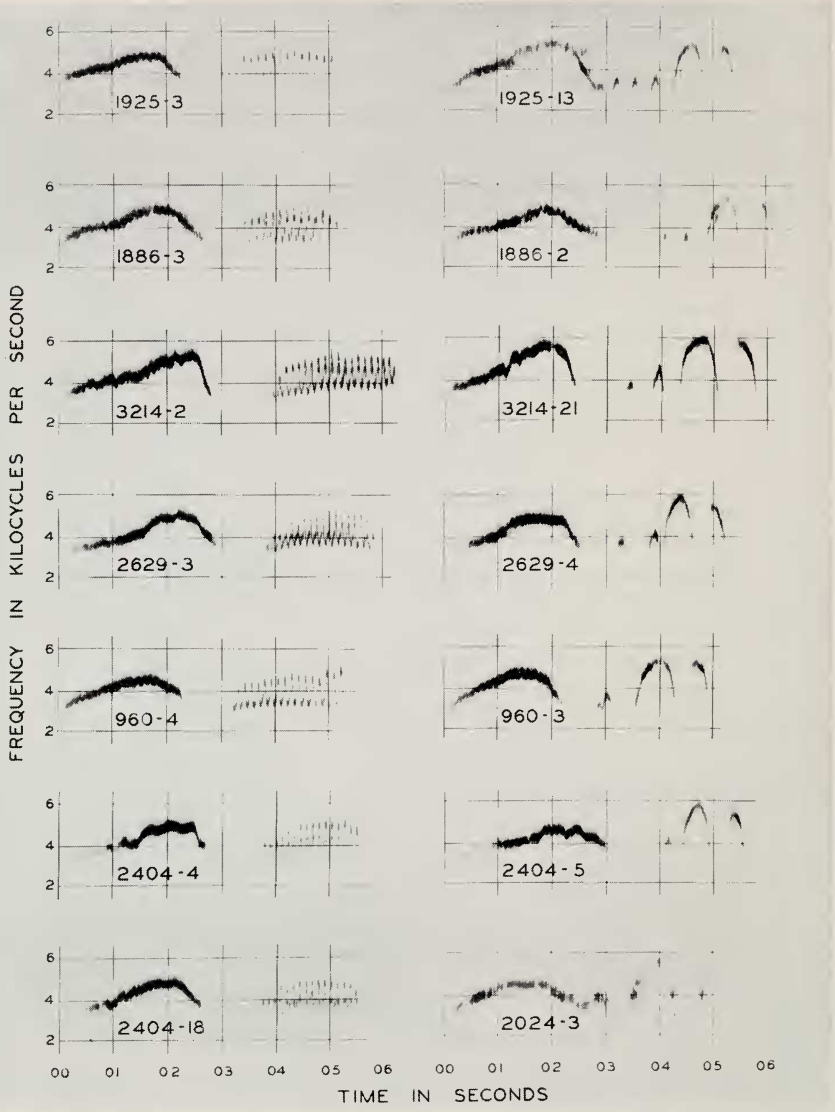

Fig. 4. Audiospectrographs of Phoebe songs; buzz songs on the left and sputter songs on the right. 1925, Columbus, Ohio, 23 May 1956; 1886, Columbus, Ohio, 19 May 1956; 3214, Franklin Co., Ohio, 15 April 1958; 2629, Columbus, Ohio, 13 May 1957; 960, Columbus, Ohio, 26 April 1954; 2404, Columbus, Ohio, 31 March 1957; 2024, Lincoln Co., Maine, 13 June 1956.

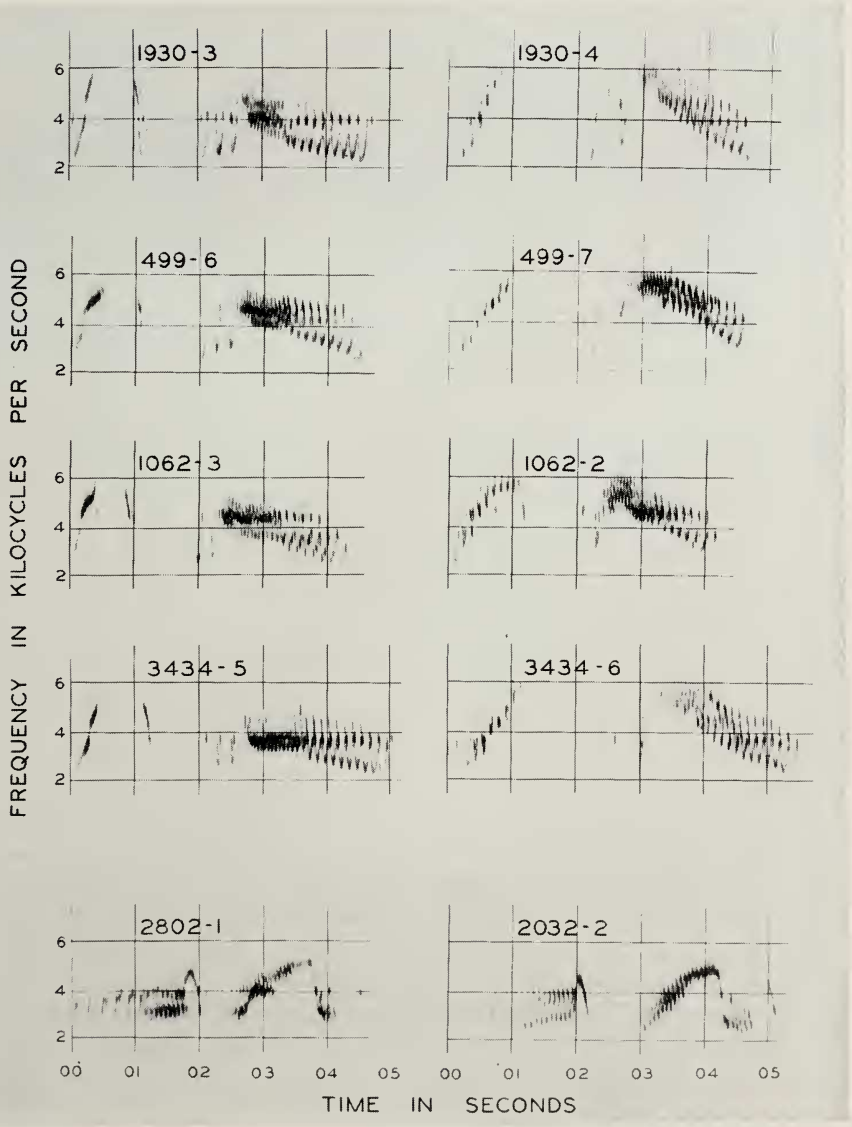

Fig. 5. Audiospectrographs of Traill's Flycatcher songs. The eight upper graphs are of the *fitz-bew* bird, with *fitts-bew* songs on the left and *fizz-bew* songs on the right; the two graphs at the bottom are of the *fee-bee-o* bird. 1930, Columbus, Ohio, 23 May 1956; 499, Columbus, Ohio, 18 May 1953; 1062, Columbus, Ohio, 22 May 1954; 3434, Reynoldsburg, Ohio, 21 May 1958; 2802, Mio, Michigan, 1 June 1957; 2032, Lincoln Co., Maine, 13 June 1956.

TABLE 3

SONG TYPES IN PHOEBE RECORDINGS

Source of Recordings	Number of Recordings	Number of Songs		
		Buzz Type	Sputter Type	Total
Ohio	12	184	99	283
Maine	3	22	30	52
Total	15	206	129	335

ear. The occurrence of these two song types in our Phoebe recordings is shown in Table 3. One of the Ohio recordings (with 3 songs) and two of the Maine recordings (with a total of 21 songs) contained only sputter songs; all the other recordings contained songs of both types. The different proportion of the two song types in the Maine and Ohio recordings is statistically significant (chi square = 9.568); the buzz type of song is more common in the Ohio birds and the sputter type is more common in the Maine birds.

The song situation in Traill's Flycatcher is much like that in the Phoebe, but with an added complication. The birds occurring in the northern part of the country, at least from New England west to the northern Great Lakes region and the upper Mississippi Valley, have a song that is generally described as *fee-bee-o*, while the birds farther south, at least in eastern United States, have a song usually described as *fitz-bew*. The songs of the *fee-bee-o* bird are apparently all of one pattern, but those of the *fitz-bew* bird are of two patterns.

The two song patterns of the *fitz-bew* bird are scarcely distinguishable by ear in the field; they differ in the character of the first part of the song. One pattern (the four upper graphs on the left in Fig. 5) begins with two short, sharp notes, and might be termed the *fitts-bew* song, while the other (the four upper graphs on the right in Fig. 5) begins with an upslurred buzz, and might be termed the *fizz-bew* song; the second part of the song is similar in the two patterns. These two song patterns are sung more or less alternately. Our 16 recordings of the *fitz-bew* bird (all from central Ohio) contain 314 songs, 225 of the *fitts-bew* type and 89 of the *fizz-bew* type; each recording contains songs of both types. Our four recordings of the *fee-bee-o* bird (three from Maine and one from Michigan) contain 37 songs, all of the same type (the two bottom graphs in Fig. 5).

Stein's work on Traill's Flycatcher (1958) indicates that where the two song forms of this bird (*fitz-bew* and *fee-bee-o*) come together in central New York they appear to be distinct species. The morphological differences between the two populations are very slight and overlapping, but the populations differ in certain aspects of nesting behavior; the birds of each population

give a characteristic reaction to songs of their own type, but not to songs of the other population.

It seems probable that the *fee-bee-o* form of this bird evolved from the *fitz-bew* form. A local population of the *fitz-bew* bird in the northeast, which had only the *fizz-bew* song, became isolated from the birds to the south and west—probably during a glacial period of the Pleistocene—and during a period of isolation its song evolved to the *fee-bee-o* type. Now, where the two populations have come together again (in central New York), they behave like distinct species. The Phoebe has probably had much the same history, but the divergence of the northeastern birds from those of the midwest does not appear to have gone as far as it has with Traill's Flycatcher.

SUMMARY

This paper presents an outline of the variation in passerine bird song, based principally on the study of tape recordings by means of a sound spectrograph. Song is the vocalization, usually given only by the male and usually more complex in character than the bird's various call notes, which serves to advertise the male, attract a female, and/or repel other males; most of the discussion in this paper refers to what is usually called the advertising song.

Both inheritance and learning play a part in the acquisition of song patterns by the individual. The early season singing of many species, as the birds are perfecting their song patterns, is somewhat primitive; once these patterns are perfected they are largely fixed for the rest of the bird's life. Occasional individuals in some species apparently learn their song from another species.

Different species of passerine birds differ in the amount of variation in the songs of a given individual and in the songs of different individuals. Individuals of some species have advertising songs of only one pattern, while those of other species may have two to many patterns; 58 patterns were found in the songs of one Lark Sparrow. In some species the songs of different individuals are of the same pattern, but in most species the songs of different individuals may differ. The variation within a species may vary from only a few patterns to a situation in which different individuals seldom if ever sing songs of the same pattern.

Data are presented on the geographic variation in the songs of Bachman's Sparrow, Song Sparrow, and Cardinal (two subspecies in each case). Studies of songs recorded in the eastern United States and Canada indicate that in at least some species the songs of different subspecies may differ; most of the intraspecific variation encountered in the songs from this area might be described as "local dialects," with birds of different areas differing in song patterns, but with few significant geographic trends evident.

Most passerine birds exhibit a daily cycle of singing activity, singing most consistently in the early morning, with the song at a minimum early in the afternoon. Some species sing a little differently at daybreak.

Song is usually associated with the breeding season, beginning in the spring and ceasing in midsummer; some species stop or reduce their singing during certain parts of the nesting cycle, and some may sing after the postnuptial molt.

The same types of song may serve all the functions of song, or different types may serve different functions. Many birds have songs of a different type than the territorial song, that are heard only infrequently ("flight" songs, "twilight" songs, etc.); the

function of these songs is not clear in every case, but in some cases they play a role in territorial defense or courtship. The females of some species sing occasionally, often in response to the male.

The large amount of intraspecific variation in many passerines complicates the problem of the student trying to learn to recognize birds by their songs. Field identification by song is based on the type of song pattern the bird sings, the quality of the song, and a knowledge of what might be expected to be singing at a given time and place. A person with an ear for pattern in bird songs will eventually be able to recognize individuals of many species by their songs; there is evidence that some birds can recognize other individuals by their songs.

Because of the role of song in species recognition, variation in song may lead to speciation; evidence is presented of such speciation trends in certain flycatchers.

LITERATURE CITED

Alexander, R. D.

1957 Sound production and associated behavior in insects. *Ohio J. Sci.*, 57:101–113.

Alexander, R. D., and T. E. Moore

1958 Studies on the acoustical behavior of seventeen-year cicadas (Homoptera: Cicadidae: *Magicicada*). *Ohio J. Sci.*, 58: 107–127.

Allard, H. A.

1930 The first morning song of some birds of Washington, D.C.; its relation to light. *Amer. Nat.*, 64:436–469.

1934 The twilight song of the Wood Pewee, *Myiochanes virens* Linnaeus. *Amer. Nat.*, 68:266–274.

Baerg, W. J.

1930 The song periods of birds of northwest Arkansas. *Auk*, 47:32–40.

Bicknell, E. P.

1884 A study of the singing of our birds. *Auk*, 1:60–71, 126–140, 210–218, 322–332.

1885 A study of the singing of our birds. *Auk*, 2:144–154, 249–262.

Blair, W. F.

1955 Mating call and stage of speciation in the *Microhyla olivacea-M. carolinensis* complex. *Evol.*, 9:469–480.

1956 Call difference as an isolation mechanism in southwestern toads (genus *Bufo*). *Tex. J. Sci.*, 8:87–106.

1958 Call difference as an isolation mechanism in Florida species of hylid frogs. *Quart. J. Fla. Acad. Sci.*, 21:32–48.

Borror, D. J.

1956 Variation in Carolina Wren songs. *Auk*, 73:211–229.

1959*a* Variation in the songs of the Rufous-sided Towhee. *Wilson Bull.*, 71:54–72.

1959*b* Songs of the Chipping Sparrow. *Ohio J. Sci.*, 59:347–356.

1960 The analysis of animal sounds. *In* Animal Sounds and Communication. Amer. Inst. Biol. Sci., Washington. pp. 26–36.

Borror, D. J., and C. R. Reese

1956 Vocal gymnastics in Wood Thrush songs. *Ohio J. Sci.*, 56:177–182.

Craig, W.

1943 The song of the Wood Pewee, *Myiochanes virens* Linnaeus: a study of bird music. *N.Y. State Mus. Bull.*, 334: 186 pp.

Dilger, W. C.
1956 Hostile behavior and reproductive isolating mechanisms in the avian genera *Catharus* and *Hylocichla*. *Auk*, 73:313–353.
Fry, H. J.
1916 A study of the seasonal decline of bird song. *Auk*, 33:28–40.
Hulme, D. C.
1950 Chaffinch (*Fringilla coelebs*) mimicking hedge-sparrow's (*Prunella modularis*) song. *Brit. Birds*, 43:222.
Koehler, O.
1951 Der Vogelgesang als Vorstufe von Musik und Sprache. *J. f. Ornith.*, 93:3–20.
Lanyon, W. E.
1957 The comparative biology of the meadowlarks (*Sturnella*) in Wisconsin. Pub. Nuttall Orn. Club, No. 1, iv + 67 pp.
1960 The ontogeny of vocalizations in birds. *In* Animal Sounds and Communication. Amer. Inst. Biol. Sci., Washington. pp. 321–346.
Lanyon, W. E., and W. R. Fish
1958 Geographical variation in the vocalizations of the Western Meadowlarks. *Condor*, 60:339–341.
Marler, P.
1952 Variation in the song of the Chaffinch (*Fringilla coelebs*). *Ibis*, 94:458–472.
Mehner, J. F.
1952 Notes on song cessation. *Auk*, 69:466–469.
Nice, M. M.
1931 Notes on the twilight songs of the Scissor-tailed and Crested Flycatchers. *Auk*, 48:123–125.
1943 Studies in the life history of the Song Sparrow II. *Trans. Linn. Soc. N.Y.*, 6:vii+328 pp.
Poulsen, H.
1951 Inheritance and learning in the song of the Chaffinch (*Fringilla coelebs* L.). *Behaviour*, 3:216–228.
1958 The calls of the Chaffinch (*Fringilla coelebs* L.) in Denmark. *Dansk. Orn. Foren. Tidsskr.*, 52:89–105.
Saunders, A. A.
1926 Additional notes on the summer birds of Allegany Park. *Roosevelt Wild Life Bull.*, 3:476–497.
1938 Studies of breeding birds in the Allegany State Park. *N.Y. State Mus. Bull.*, 318; 160 pp.
1947 The seasons of bird song. The beginning of song in the spring. *Auk*, 64:97–107.
1948*a* The seasons of bird song—the cessation of song after the nesting season. *Auk*, 65:19–30.
1948*b* The seasons of bird song. Revival of song after the postnuptial molt. *Auk*, 65:373–383.
Smith, R. L.
1959 The songs of the Grasshopper Sparrow. *Wilson Bull.*, 71:141–152.
Stein, R. C.
1958. The behavioral, ecological, and morphological characteristics of two populations of the Alder Flycatcher, *Empidonax traillii* (Audubon). *N.Y. State Mus. and Sci. Serv. Bull.*, 371; 63 pp.

Tasker, R. R.
1955 Chipping Sparrow with song of Clay-colored Sparrow at Toronto. *Auk*, 72:303.
Tavolga, W. N.
1956 Visual, chemical and sound stimuli as cues in the sex discriminatory behavior of the gobiid fish *Bathygobius soporator*. *Zoologica*, 41:49–65.
1958*a* The significance of underwater sounds produced by males of the gobiid fish, *Bathygobius soporator*. *Physiol. Zool.*, 31:259–271.
1958*b* Underwater sounds produced by males of the blenniid fish, *Chasmodes bosquianus*. *Ecol.*, 39:759–760.
Thorpe, W. H.
1951 The learning ability of birds. *Ibis*, 93:1–52, 252–296.
1954 The process of song-learning in the Chaffinch as studied by means of the sound spectrograph. *Nature*, 173:465–469.
1956 The language of birds. *Sci. Amer.*, 195:128–138.
1958*a* The learning of song patterns by birds, with especial reference to the song of the Chaffinch, *Fringilla coelebs*. *Ibis*, 100:535–570.
1958*b* Further studies on the process of song learning in the Chaffinch (*Fringilla coelebs gengleri*). *Nature*, 182:554–557.
VanTyne, J., and A. J. Berger
1959 Fundamentals of ornithology. John Wiley and Sons, New York. x+624 pp.
Vaurie, C.
1946 Early morning song during middle and late summer. *Auk*, 63: 163–171.
Walker, T. J., Jr.
1957 Specificity in the response of female tree crickets (Orthoptera, Gryllidae, Oecanthinae) to calling songs of the males. *Ann. Ent. Soc. Amer.*, 50:626–636.
Weeden, J. S., and J. B. Falls
1959 Differential response of male Ovenbirds to recorded songs of neighboring and more distant individuals. *Auk*, 76:343–351.
Wright, H. W.
1912 Morning awakening and even-song. *Auk*, 29:307–327.
1913 Morning awakening and even-song. *Auk*, 30:512–537.

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